



U.S. Department of Agriculture
Animal and Plant Health Inspection Service
Wildlife Services

U.S. Government Publication



Den use and heterothermy during winter in free-living, suburban striped skunks

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Many mammals use heterothermy to meet challenges of reduced food availability and low temperatures, but little is known about the prevalence of heterothermy in wild mesocarnivores. We monitored body temperature (T_b) in free-living striped skunks (*Mephitis mephitis*) through winter 2015–2016 in suburban Flagstaff, Arizona, a high-elevation site that experiences temperate winters. Subcutaneous T_b and heterothermy index (HI) were significantly affected by ambient temperature, and varied significantly across 7 skunks in midwinter. Twenty-one of 36 (58%) unique diurnal dens used by skunks were associated with human structures, and although females were found in dens under houses more than expected compared to males, we found little evidence that skunks selected dens where they could access anthropogenic heat sources. This is the 1st study to document T_b variation over winter in free-living striped skunks. Our results are consistent with 2 previous studies of captive skunks in documenting considerable variation among individuals in the extent of heterothermy. If reduced T_b during heterothermy alters rate of viral replication, variation among individual skunks could have implications for the maintenance and spread of diseases like rabies.

Key words: den, heterothermy, heterothermy index, *Mephitis*, rabies, torpor

The high metabolic costs of endothermy are difficult to meet during times of food scarcity especially when ambient temperature (T_a) falls far below body temperature (T_b). For mammals living at mid- to high latitudes, the period of food scarcity often coincides with low T_a , thereby increasing metabolic costs at the same time that food is scarce. A combination of behavioral and physiological mechanisms are employed by mammals to cope with these challenges, including reduced activity, retreat to insulated dens, communal denning, and lowering body temperature (T_b) and metabolism through daily torpor or seasonal hibernation (Hayes 2000; Humphries et al. 2005; Ruf and Geiser 2015). The tendency to enter torpor, and the depth and length of that torpor, varies considerably across mammalian species, and is associated with environmental conditions, taxonomic affinity, and body size (Geiser and Ruf 1995; Geiser 1998).

Within the mammalian Order Carnivora, torpor is relatively rare, documented only in bears (*Ursus americanus* and *Ursus*

arctos—Tietje and Ruff 1980), American and European badgers (*Taxidea taxus* and *Meles meles*—Harlow 1981; Fowler and Racey 1988), and striped skunks (*Mephitis mephitis*—Mutch and Aleksiuik 1977; Hwang et al. 2007). The minimum T_b of striped skunks is the lowest recorded for carnivores (26°C—Hwang et al. 2007). Only 2 studies have documented T_b in striped skunks over winter, and both relied on captive skunks held in outdoor enclosures. Mutch and Aleksiuik (1977) measured T_b of 3 male skunks caged separately in outdoor enclosures in Canada from December through March and found that the 3 animals showed different patterns of T_b regulation, with 1 animal allowing T_b to regularly drop to 28°C, while another never decreased T_b < 32°C and the third never < 34°C. Hwang et al. (2007) investigated the effect of communal denning on torpor by comparing T_b in 4 groups of 4 individual striped skunks each housed communally, to that of 4 individuals housed in separate dens, again in outdoor enclosures in Canada. In this case, all solitary denning skunks

regularly entered torpor, whereas communally denning animals did so infrequently.

We know little about whether animals that rely on torpor vary that response in human-modified habitats, where human-provided foods may buffer seasonal food scarcity and where human structures may provide den sites with different thermal properties. Along with raccoons (*Procyon lotor*), striped skunks are often one of the most abundant mesocarnivores in human-modified landscapes (Rosatte et al. 1991; Broadfoot et al. 2001), presumably because of the increased availability of anthropogenic foods and den sites (Prange et al. 2004). Skunks often den in human structures, including sheds, out-buildings, and decks (Verts 1967; Houseknecht and Tester 1978; Larivière et al. 1999; Hwang et al. 2007), but also under the foundations of houses (Theimer et al. 2016) where they could potentially access pockets of heat generated near water pipes or heating ducts.

In this study, we investigated winter den use and the temporal pattern of T_b through winter in wild, free-living skunks in a suburban environment. Based on previous studies, we hypothesized that individuals that denned solitarily would regularly enter torpor, whereas those denning communally would do so infrequently. We predicted that heterothermy would be affected by T_a , which directly influences the cost of endothermy, and by snow cover, which limits access to forage. We also predicted that skunks would preferentially select crawl spaces under houses as dens in order to exploit anthropogenic sources of heat.

METHODS

Study area.—Flagstaff, Arizona, United States (35.185307°N, -111.651910°W) lies at 2,100 m elevation and experiences a seasonal climate with monsoonal rainfall during the warm summer months and subfreezing temperatures and snow during winter. We focused our study in an approximately 3-km² suburban area that included moderate- to low-density housing interspersed with golf courses, small ponds and reservoirs, and small (typically < 2 ha) patches of native ponderosa pine (*Pinus ponderosa*) habitat.

Capture, surgery, and recapture.—Skunks were captured in cage traps between 30 October and 12 November 2015 at 2 winter den locations discovered during earlier studies (Theimer et al. 2016). We implanted data loggers (iButton Thermochron DS1922L; Maxim Integrated Products, San Jose, California) subcutaneously between the shoulder blades in 15 skunks (8 males and 7 females). Data loggers weighed approximately 5 g when sealed with a protective wax coating and were programmed to record temperature ($\pm 0.5^\circ\text{C}$) every 30 min. Four of the 15 animals were implanted with a 2nd iButton into the abdominal cavity. While under anesthesia for surgeries, skunks were weighed, measured, fitted with proximity-sensing radiocollars (Sirtrack, Havelock, New Zealand), and a uniquely numbered aluminum ear tag was placed in each ear. Radiocollars weighed approximately 40 g and transmitted a unique VHF signal for radiotracking and also sent and received unique UHF

signals that recorded the date, time, and identity of any other radiocollared skunk that came within 1 m. This study followed ASM guidelines for the use of wild mammals in research (Sikes et al. 2016) and was approved by the NAU Institutional Animal Care and Use Committee (Protocol 11-002).

We radiotracked skunks during the day every 1–3 days using a vehicle-mounted omnidirectional antenna followed by homing-in using a handheld Yagi antenna. Beginning on 22 January 2016, we recaptured skunks using cage traps or handheld nets, removed their radiocollars, surgically explanted the data loggers, and then released them.

Analyses.—The expression of torpor has traditionally been identified based on depression of T_b below some threshold (Barclay et al. 2001; Willis and Brigham 2003; Brigham et al. 2011). Recently, it has been argued that such thresholds are arbitrary and prevent the inclusion of animals typically regarded as “homeotherms” in comparative studies (Boyles et al. 2011a). Instead, a simple comparative metric, the heterothermy index (HI), was proposed to describe temporal variation in T_b of an individual during a given time frame (Boyles et al. 2011b). Because HI may not distinguish between deep or short and long or shallow torpor bouts (Ruf and Geiser 2015), we used 3 approaches to examine heterothermy in free-living skunks: 1) torpor as defined by previously established thresholds (31°C—Hwang et al. 2007), 2) minimum daily diurnal T_b (MDDT_b; minimum T_b measured between 0800 and 1800 h each day, when skunks remain in their den), and 3) the HI. We calculated daily HI as described in Boyles et al. (2011b) where

$$\text{HI} = \sqrt{\frac{(T_{\text{bmod}} - T_{\text{bi}})^2}{(n - 1)}}$$

and T_{bmod} is the mode of all recorded temperatures and T_{bi} is the temperature at time i .

To evaluate the utility of subcutaneous implants as a proxy for core T_b , we compared T_b , HI, and MDDT_b measured subcutaneously versus abdominally using linear regression analysis. We then used linear mixed models to examine how sex, T_a , and snow cover influenced subcutaneous HI (log-transformed) and subcutaneous MDDT_b (separate model; squared-transformation). We allowed individuals to vary in both their intercepts and the slope of their response to T_a (i.e., a random intercept and slope model). Analyses were implemented using Proc Mixed in SAS, fitted using REML; our model specified heterogeneity in the covariance structure among the snow-cover groups. Mean-level effects were evaluated using F -tests (type III sums of squares) and denominator degrees of freedom for fixed effects using the Kenward-Roger method (SAS Institute, Cary, North Carolina).

To test for differences among individuals in their use of heterothermy in midwinter, we compared daily subcutaneous HI values for the 40 days from 15 December to 23 January using 1-way ANOVA followed by Tukey’s test for differences among individuals in SPSS. Given that 1 HI value was calculated for each day for each skunk and T_a varied from day to day, we assumed HI values for the same skunk on different days were

independent. We included in this analysis the 40-day period from 28 February to 8 April for the 1 skunk (female 808) for which we had T_b data extending into the early spring to determine whether tendency for heterothermy differed between mid-winter and spring within this individual.

We used a contingency table chi-square test to evaluate differences between sexes in their likelihood to den under houses rather than in other dens. For animals that denned under houses, we compared HI and MDDT_b values when those animals were under houses to the values when they were denned elsewhere using a *t*-test in SPSS.

To determine whether MDDT_b was more likely to occur during the nocturnal (active) phase or the diurnal (inactive) phase, we divided each 24-h period into 2 parts, 0600–1759 h and 1800–0559 h, and then used a chi-square test to assess whether MDDT_b was equally likely to occur in both phases (Hwang et al. 2007).

RESULTS

We implanted temperature loggers subcutaneously in 15 adult striped skunks (7 males and 8 females) and abdominally in 2 of those males and 2 of those females. One of the 2 males with both implants died 8 days after release. Out of the total 15 skunks with subcutaneous implants, we were able to regularly radiotrack 8 and recovered temperature loggers from 7.

Subcutaneous T_b versus abdominal T_b .—For the 3 skunks from which we recovered both abdominal and subcutaneous temperature loggers, we found that subcutaneous T_b was correlated with abdominal T_b (female 545: $r^2 = 0.40$, female 506: $r^2 = 0.53$, male 556: $r^2 = 0.17$, all 3 combined $r^2 = 0.49$) and daily subcutaneous HI was correlated with the abdominal HI (female 545: $r^2 = 0.71$, female 506: $r^2 = 0.78$, male 556: $r^2 = 0.09$, 3 combined $r^2 = 0.71$; Supplementary Data SD1). Some of the differences between subcutaneous T_b and abdominal T_b reflected the more rapid cooling and delayed warming of the periphery relative to the body core. When T_b was measured across the entire 24-h period, there were often outliers with lower than predicted subcutaneous T_b at relatively warm core T_b . These outliers occurred when animals were active at night under cold, snowy conditions, presumably because the hairless incision sites on their backs were exposed. The lower within-animal correlations for T_b in the male were associated with low variability, as abdominal T_b in this animal was never < 34.6°C. Thus, subcutaneous T_b generally reflected the temporal pattern of abdominal T_b , although subcutaneous T_b was often 2–3° lower than corresponding abdominal T_b (Supplementary Data SD2).

Previous studies have utilized core $T_b < 31^\circ\text{C}$ as a threshold for identifying torpor in skunks (Hwang et al. 2007). The distribution of T_b (core or subcutaneous) was unimodal but skewed to the left (with the exception of skunk 556) and the distribution for daily HI was unimodal but right skewed. Thus, we were unable to identify new effective criteria (break points) for identifying when animals were torpid and instead utilize the previously applied threshold approach. Using the 31°C

threshold definition of torpor in skunks, 1 of the 3 skunks that had both abdominal and subcutaneous T_b loggers entered torpor on 11 days between 29 November 2015 and 1 February 2016 based on their abdominal T_b , with the lowest T_b of 28.6°C recorded on 2 of those days. Duration of $T_b < 31^\circ\text{C}$ varied from 2 to 10 h ($\bar{X} = 5.1 \pm 2.5$ SD, mode = 4.5) with 9 of 11 torpor bouts initiated during the day between 0830 and 1700 h, and 2 between 2000 and 2100 h.

Subcutaneous body temperature.—Similar to what we observed for abdominal T_b , subcutaneous T_b varied among animals, as well as within animals (Fig. 1). The linear mixed model for MDDT_b showed a significant positive effect of mean daily T_a (estimate \pm SE = 5.1 ± 1.4 , $F_{1,16} = 13.42$, $P = 0.002$), but no effect of snow cover (32.7 ± 42.9 , $F_{1,11} = 0.58$, $P = 0.46$) or sex (29.1 ± 49.6 , $F_{1,11} = 0.32$, $P = 0.57$). Similarly, the linear mixed model for daily HI indicated a significant negative effect of mean daily T_a (estimate \pm SE = -0.011 ± 0.004 , $F_{1,12} = 8.71$, $P = 0.01$), but not snow cover (-0.09 ± 0.06 , $F_{1,8} = 2.08$, $P = 0.19$) or sex (0.06 ± 0.06 , $F_{1,8} = 1.02$, $P = 0.34$).

Subcutaneous HI varied significantly among individuals in midwinter ($F_{7,312} = 40.4$, $P < 0.001$; Fig. 2). The same female that showed the highest daily HI in midwinter (808) recorded HI values in March lower than any skunk during midwinter, indicating a major shift in the tendency to depress T_b in this individual (Figs. 1 and 2).

All skunks showed a diel pattern of T_b fluctuation similar to that expected at other times of the year, with the number of times low temperatures were recorded between 0600 and 1759 h significantly greater than expected ($X^2_1 = 162$, $P < 0.0001$), and the number of times high temperatures were recorded significantly less than expected during that period ($X^2_1 = 254$, $P < 0.0001$; Fig. 3). Individual skunks did not consistently reach maxima and minima at the same time each day, nor were skunks reaching maxima or minima at the same times on any 1 day.

Den use.—We tracked 8 skunks to their diurnal dens 160 times between 29 November 2015 and 9 February 2016. Individual skunks used from 3 to 6 ($\bar{X} = 4.5 \pm 1.2$ SD) unique dens during this time period, but often moved among the same dens, so the number of den changes was higher, ranging from 5 to 9 ($\bar{X} = 7.0 \pm 1.8$ SD). Out of 36 unique diurnal dens, 20 (56%) were associated with human structures (sheds, decks, garages) and 16 were in rocks, culverts, or logs. Only 1 type of den could have allowed skunks access to crawl spaces and anthropogenic sources of heat. These dens were under the wooden decks of houses with the radio signal emanating from near the house foundation. In these cases, it was impossible to determine whether the skunk was under the deck, within the house foundation, or in a burrow below the foundation. Of the 8 skunks we tracked, 3 were never recorded in this den type and 3 were found in this den type on < 15% of occasions. Females were found in this den type significantly more than expected by chance than males ($X^2_1 = 7.1$, $P < 0.01$). We recovered subcutaneous temperature data from 1 female that regularly used a den under a house. HI and MDDT_b values for this female did not differ between the 10 days when she was denned under the

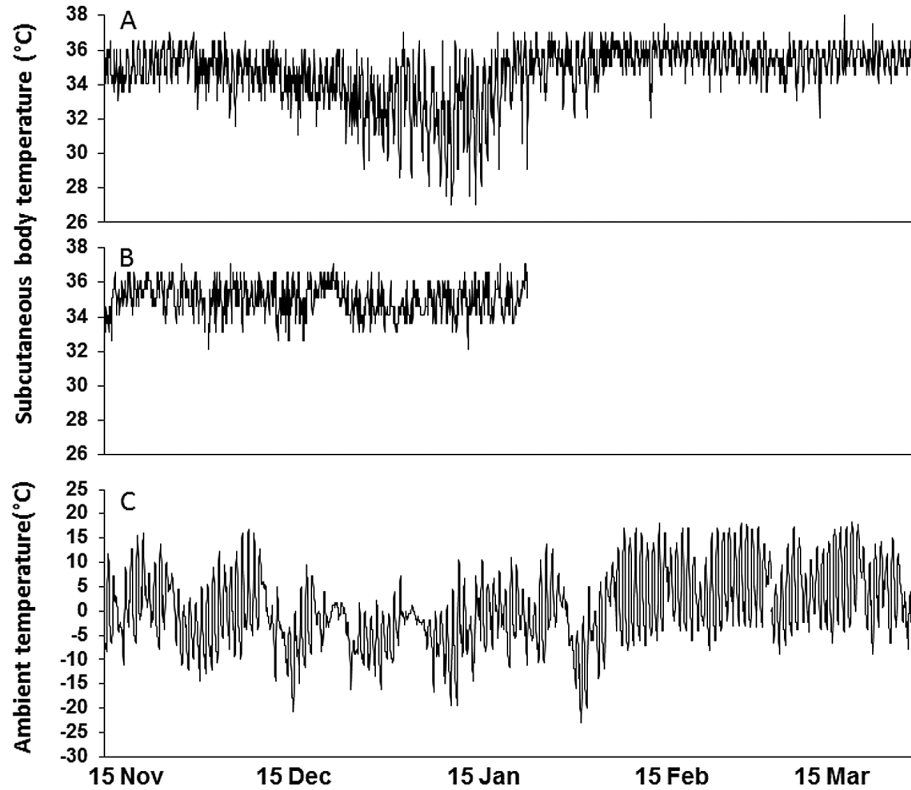


Fig. 1.—Subcutaneous T_b of female striped skunk (*Mephitis mephitis*) 808 (A) and male 556 (B) and hourly ambient temperature (C) from 15 November 2015 to 31 March 2016 in suburban Flagstaff, Arizona, illustrating extremes in subcutaneous T_b variation among the 7 skunks studied.

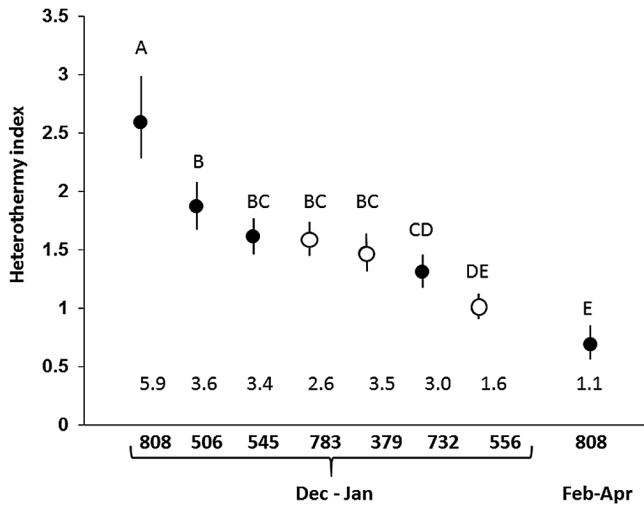


Fig. 2.—Mean and 95% CI of daily heterothermy index (HI) for 7 striped skunks (*Mephitis mephitis*) calculated over the 40 days from 15 December 2015 to 23 January 2016 and for 1 of those skunks (808) for the 40-day period from 28 February to 8 April 2016 in Flagstaff, Arizona, United States. Open symbols are males, closed symbols are females. Skunks with the same letter are not statistically different at $P < 0.05$ based on Tukey’s post hoc tests. Maximum HI values recorded for each skunk T_b during the 40-day period are given above the x-axis.

house compared to the subsequent 10 days when she denned in a culvert with 2 other females ($\bar{X} \pm SE$ HI house den = 1.5 ± 0.2 , culvert = 1.4 ± 0.2 , $t_{20} = 1.2$, $P = 0.23$; $\bar{X} \pm SE$ MDDT_b house den = 33.8 ± 0.4 , culvert = 34.6 ± 0.4 , $t_{20} = 1.5$, $P = 0.13$).

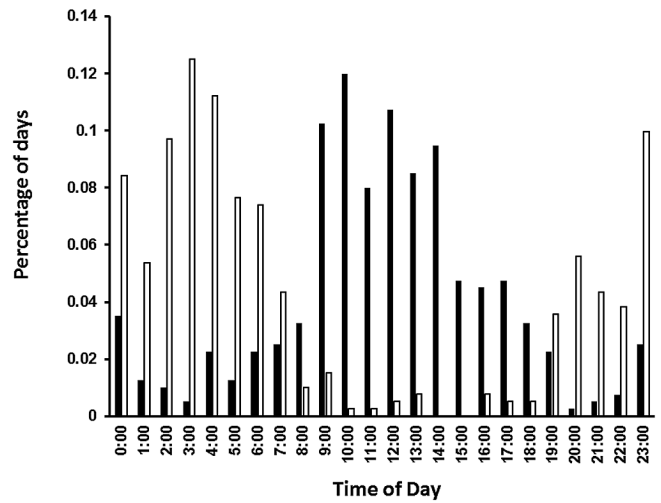


Fig. 3.—The percentage of days 7 striped skunks (*Mephitis mephitis*) recorded maximum (open bars) and minimum (solid bars) subcutaneous T_b at different times of the day from 1 December 2015 to 31 January 2016 in Flagstaff, Arizona, United States.

DISCUSSION

We documented that wild, free-living striped skunks living at a relatively low-latitude, high-elevation site varied significantly in their degree of heterothermy. Our results were similar to those of Mutch and Aleksiuik (1977), who found that 3 captive male skunks housed in outdoor enclosures in Canada showed a range of temperature responses, with 1 animal regularly dropping T_b to 28°C, while others maintained relatively high T_b

throughout the study. Hwang et al. (2007) likewise reported that some captive striped skunks regularly entered torpor while others rarely did. Unlike that study, however, none of the skunks we studied showed a regular and consistent daily pattern of torpor. Instead, some individuals lowered T_b frequently at irregular intervals, while others rarely decreased T_b . The 1 female we followed through winter and into early spring showed the most consistent pattern of T_b reduction and the highest HI value during winter that contrasted sharply with the consistently high and relatively constant T_b that animal exhibited in spring. Even relatively small and infrequent drops in T_b , like those shown by many of the skunks we studied, could result in energy savings. For example, Harlow (1981) estimated for the American badger that a daily reduction in body temperature of 1.7°C could result in a savings of 17 g fat/day. Although it is uncertain for this species, energetic savings in skunks could be much higher than predicted by T_b alone if they utilize temperature insensitive metabolic suppression as is seen in the black bear (*U. americanus*—Tøien et al. 2011) and the arctic ground squirrel (*Urocitellus parryii*—Buck and Barnes 2000).

Communal denning and huddling behavior should reduce thermal costs through shared body heat and reduced surface area:volume ratios (Vickery and Millar 1984; Bazin and MacArthur 1992; Hayes et al. 1992). During winter, communal denning or nesting occurs across the heterothermic spectrum, from species that never utilize heterothermy (Williams et al. 2013) to those that are classified as obligate seasonal hibernators (Arnold 1988; Lee et al. 2015). In socially hibernating marmots, all individuals within a hibernacula exhibit deep torpor ($T_b < 10^\circ\text{C}$) with close synchrony in the timing of torpor and arousal cycles (Arnold 1988; Lee et al. 2015). In contrast, Hwang et al. (2007) found that captive striped skunks housed individually regularly entered torpor while skunks sharing communal dens with other skunks rarely did so. In the present study, during a 26-day period when 2 females denned together and a subsequent 10-day period when those 2 were joined by a 3rd female, all 3 females continued to show their own unique pattern of T_b variation, with only 1 individual regularly entering torpor. Male skunks are more often reported as denning solitarily in winter (Verts 1967; Sunquist 1974; Houseknecht and Tester 1978) and we documented a male denning with other skunks only once. In a previous study conducted in the same neighborhood of Flagstaff with a much larger sample of radio-collared animals, we likewise found males rarely denned with other skunks during the latter half of December (Theimer et al. 2016). These data suggest that our male skunks were likely denning solitarily for at least part of the winter, yet all 3 males tended to have relatively constant T_b throughout December and January. In contrast, Hwang et al. (2007) found that solitary males entered torpor regularly. Thus, the pattern of T_b fluctuation in solitary versus communally denning skunks reported for captive skunks in Canada differs from that of the wild skunks we studied in Arizona.

All skunks in our study showed a diel T_b cycle generally similar to that of skunks during the active season, with highest T_b reached during the night or immediately before dawn

and lowest T_b during the day or late afternoon. Similar patterns of T_b in winter were noted by Mutch and Aleksiuik (1977) and for movements within winter dens by Sunquist (1974). As in Mutch and Aleksiuik (1977), skunks showed considerable variation in the timing of diel maxima and minima, both between individuals on the same day and for the same animal on different days. Hwang et al. (2007) also found that grouped individuals entered torpor during the day and aroused in the evening, but in that study solitary animals did the opposite, a pattern we never encountered. This difference could be due to the fact that the skunks in Hwang et al. (2007) had access only to an outdoor enclosure with no food available for the 117 days after 30 November, whereas our free-ranging skunks continued to move among dens, and presumably forage, throughout the winter. Thus, the shift in daily patterns of heterothermy documented by Hwang et al. (2007) may reflect the pattern typical in areas where winter activity is greatly reduced and skunks remain inactive in winter dens for extended periods, but not that of areas like ours where skunks remain more active through the winter. Alternatively, this difference may be an artifact of captivity, as several species of rodents are known to switch their temporal niches from diurnal to nocturnal, or occasionally vice versa, when moved from field conditions into the lab (e.g., Hut et al. 2012; Tachinardi et al. 2015).

Suburban habitats offer a diversity of den sites differing from those found in rural areas or wild lands, including some that could have different thermal characteristics (Bevanger and Broseth 1998). Skunks have been documented using human structures as dens in many other studies (Verts 1967; Houseknecht and Tester 1978; Larivière et al. 1999; Hwang et al. 2007), primarily sheds and outbuildings, and over one-half of the winter dens we found were also under decks, garages, or sheds. We found little evidence that skunks were preferentially seeking out diurnal dens where they could access anthropogenic sources of heat. One caveat of our study, and an opportunity for future studies, was that we were not able to place data loggers inside of dens so we do not know how the thermal properties of different den types vary.

The factors that ultimately trigger appropriate physiological and behavioral responses to the onset of winter in striped skunks remain unknown. Reduced food availability does not appear to be the trigger for northern latitude striped skunks, as captive animals kept on ad libitum food still entered a period of hypophagy and reduced activity between October and December (Aleksiuik and Stewart 1977). Although T_a was not strongly correlated with either surface activity (Mutch and Aleksiuik 1977) or the tendency to den communally (Theimer et al. 2016) in other studies, we found significant relationships between T_a and several measures of heterothermy, suggesting the variation in T_b in the skunks we studied may be linked to surface temperature. For European badgers, Fowler and Racey (1988) hypothesized that photoperiod may be the ultimate cue for winter denning, with temperature and food supply as mediators but not the primary driver. Striped skunks at our high-elevation Arizona site would experience markedly different photoperiod in winter than skunks in Canada, but showed similar patterns of T_b

variation, at least in those denning communally. A few hundred kilometers to the south of our site, striped skunks experience mild, desert winters and are presumably active year-round, as they are in similar habitat in Texas (Doty and Dowler 2006). Comparison of winter behavior in these relatively nearby northern and southern Arizona striped skunk populations offers the possibility to investigate the genetic and ecological drivers for plasticity in T_b regulation that appears common in skunks and other carnivores.

Skunks are one of the most important terrestrial reservoirs for rabies in the United States (Monroe et al. 2016). If the reduction in T_b in wintering skunks can slow viral replication, as it can in hibernating bats (Sulkin et al. 1960; George et al. 2011; Davis et al. 2016), heterothermy may allow skunks to maintain the virus through winter when surface activity and potential for disease spread through contacts across the landscape is reduced. The variation among individuals in the frequency and magnitude of T_b reduction that we documented could be especially important in this case, by leading to variable incubation periods among individuals that acquire infections prior to the onset of winter, and may contribute to spring pulses of rabies cases observed in surveillance data (Gremillion-Smith and Woolf 1988).

ACKNOWLEDGMENTS

We thank S. Nichols, D. Dillon, K. Davis, A. Dyer, T. Rizza, and V. Zhang for assistance during surgeries and in the field. This project was funded in part through a grant from the Arizona Biomedical Research Commission to TCT. Author contributions: TCT developed concept, captured animals, collected field data, aided with surgeries, analyzed data, drafted figures, and wrote the initial manuscript; CTW helped refine concept, captured animals, performed surgeries, analyzed data, drafted figures, and wrote the initial manuscript; SRJ, ATG, DLB, and CLB helped refine concept, provided key logistical support, and commented on earlier drafts of the manuscript.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Parameter estimates \pm SE (P -values in brackets) for linear regressions of subcutaneous versus abdominal minimum daily diurnal body temperature (MDDT_b) and heterothermic index (HI) within 3 striped skunks (*Mephitis mephitis*; female 545, female 506, and male 556) and with all individuals combined based on data collected in Flagstaff, Arizona in winter 2015–2016.

Supplementary Data SD2.—The relationship between (A) subcutaneous MDDT_b and abdominal MDDT_b, and (B) subcutaneous HI and abdominal HI in 3 striped skunks (*Mephitis mephitis*) implanted with both subcutaneous and abdominal T_b loggers. (C) Abdominal (black line) and subcutaneous (gray line) temperatures recorded hourly from female striped skunk 506 between 2400 h 14 January and 2400 h 24 January 2016 in suburban Flagstaff, Arizona, United States.

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Submitted 12 September 2016. Accepted 31 January 2017.

Associate Editor was Perry Barboza.